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# Responses of mustelids and small mammal prey to combined retention on clearcuts: Woody debris, green trees, and riparian structures

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ABSTRACT

Small mustelids such as the American marten (*Martes americana*) and short-tailed weasel (*Mustela erminea*) are important furbearers in temperate and boreal forests and are negatively affected by clearcutting. A major prey species, the southern red-backed vole (*Myodes gapperi*), also disappears from clearcuts and does not return to abundance levels of uncut forest for many decades. We tested the hypotheses (H) that on newly clearcut sites, ($H_1$) the presence of small mustelids, ($H_2$) abundance, species richness, and species diversity of the forest-floor small mammal community, and ($H_3$) reproduction of the major species: *M. gapperi* and the deer mouse (*Peromyscus maniculatus*), would be greater on sites with combined retention treatments of woody debris piles, riparian, and green-tree retention than on sites with no retention. A fourth hypothesis ($H_4$) predicted that the above response variables on sites with combined structural retention would be comparable to or higher than those in uncut old-growth forest. Mustelid presence and populations of forest-floor small mammals were sampled on five replicated ($n = 4$) treatment sites from 2017 to 2020 in south-central British Columbia, Canada.

Mean presence (index of activity patterns) of mustelids was statistically similar among sites but in the combined treatments was 1.4 to 2.9 times higher than that in the dispersed (no retention) and uncut forest sites and was likely biologically important. Mustelid presence was particularly evident in the debris piles and riparian sites. Mean abundance of *M. gapperi* was 11.1 to 16.6 times higher in the combined retention and uncut forest sites than the dispersed sites. Mean abundance of *P. maniculatus* was higher in the dispersed than uncut forest, but similar in the combined retention to these treatments. Mean total abundance, species richness, and species diversity of eight small mammal species were all higher (1.3 to 1.6 times) in the combined retention sites than the dispersed and uncut forest sites. Although not formally significant ($P = 0.08$), results for mustelid presence tended to support $H_1$ that these small carnivores would occur more frequently on sites with combined structural treatments than the dispersed and uncut forest sites. The overall high total numbers (and species richness and diversity) of small mammal prey species supported $H_2$ that abundance would be greater on sites with the combined retention than on the dispersed sites with no retention. Reproduction and survival followed the pattern of abundance for the major species, and hence $H_3$ was supported. Higher mean total abundance in combined retention sites than in uncut forest supported $H_4$ in 2017–2018 but not in 2019–2020 when an influx of generalist species increased total abundance in the dispersed sites. This study is the first to measure the responses of small mustelids and small mammal prey species to combined structural retention. One or more of these retention treatments is highly recommended during most harvesting regimes in these forests.

## 1. Introduction

The American marten (*Martes americana*) and short-tailed weasel (*Mustela erminea*) are common inhabitants of forested North America (Simms, 1979; Buskirk and Zielinski, 2003). Marten occupy forest landscape mosaics that include older (>80 years) conifer-dominated stands with relatively high levels of canopy closure (minimum of 30%–50%), particularly spruce (*Picea* spp.) and true fir (*Abies* spp.), as well as riparian forests (Buskirk and Powell, 1994; Thompson and Harestad, 1994; Roloff et al., 2020). A major prey species for marten is the southern red backed vole (*Myodes gapperi*) which is an important indicator species of closed-canopy forest conditions in managed

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landscapes (Merritt, 1981). The short-tailed weasel is broadly distributed in various forest successional stages, edge habitats, and riparian woodlands where dense understory vegetation provides habitats for small mammal prey, particularly microtine voles (King, 1983; King and Powell, 2007). The long-tailed weasel (*Mustela frenata*) also occupies these habitats and has a wider range of prey species that include voles as well as deer mice (*Peromyscus* spp.), chipmunks (*Neotamias* spp.), and other less common rodent and avian species (Sheffield and Thomas, 1997).

Large openings in forests created by clearcutting has reduced the abundance of small mustelids because of a loss of food, cover, and other components of stand structure (Hargis et al., 1999; Fisher and Wilkinson, 2005; Thompson et al., 2012; Lavoie et al., 2019). Loss of security cover on clearcuts, in particular, is crucial as these mustelids may be prey species for other carnivores (Buskirk and Zielinski, 2003; Linnell et al., 2017). In terms of a major prey species, *M. gapperi* also disappears from clearcuts within a year of harvest, presumably because of a loss of food and cover, at least in coniferous and mixed forests in western North America (Zwolak, 2009). *M. gapperi* does not return to abundance levels of mature or old-growth forest for many decades after clearcutting (Fuller et al., 2004; St-Laurent et al., 2008). However, other forest-floor small mammals such as the deer mouse (*P. maniculatus*), chipmunks, some species of *Microtus* voles, and *Sorex* shrews occur as habitat generalists on clearcuts for variable periods (Fisher and Wilkinson, 2005; Zwolak, 2009).

Thus, we ask what enhancements of stand structure could be done at the time of clearcutting to provide food and cover for mustelids and prey species immediately thereafter? Structures built from post-harvest woody debris (e.g., piles and windrows) at the time of forest harvesting and log processing have generated some important networks for mustelids and prey species (Sullivan et al., 2012, 2017a; Seip et al., 2018). Both marten and weasels use coarse woody debris (CWD) as cover and focal points for finding prey species such as *M. gapperi* and other small mammals (Lisgo et al., 2002; McComb, 2003; Andruskiw et al., 2008).

Aggregated retention of patches or "islands" of mostly live timber may be left on some clearcut sites, usually along riparian zones and as forest reserves, to provide at least some forest cover and to act as critical habitats for wildlife (Darveau et al., 2001; Rosenvald and Lohmus, 2008). Short-term results (3 years after clearcutting) found that *M. gapperi*, total forest-floor small mammals, and presence of small mustelids were maintained in patches ranging from 0.3 to 20.0 ha (Sullivan and Sullivan, 2020). Although these results are encouraging, the more common type of green-tree retention (GTR) involves dispersed and aggregated harvesting patterns where some green trees are conserved while the majority of standing timber is harvested (Franklin et al., 1997; Gustafsson et al., 2012). Indeed, economic constraints suggest that clearcutting may continue as the dominant harvest system in temperate and boreal forests with relatively low amounts of GTR (e.g. $< 5$ $m^2$/ha basal area or 5% uncut forest).

A third source of structural retention on new clearcuts could be enhanced riparian management whereby trees, shrubs, and herbaceous vegetation along a stream channel might be conserved relatively intact. Riparian zones usually occupy only 1–2% of a forested landscape but provide habitat for $>$ 50% of wildlife species owing to their diversity of biological and physical features (Kauffman et al., 2001; Anthony et al., 2003).

Linear habitats along forest- and field-edges and riparian areas provide relatively secure pathways for dispersal of small mustelids since they may be prey species for other carnivores (Buskirk and Zielinski, 2003; Linnell et al., 2017; Mougeot et al., 2020). Although higher levels were expected in riparian habitats because of greater structural retention, a review by Anthony et al. (2003) concluded that studies of abundance and species diversity of forest-floor small mammals have not shown consistent differences between riparian and upland areas. In addition, Marczak et al. (2010) concluded from their *meta*-analysis that abundance of small mammals did not differ significantly between riparian buffers and reference sites.

Thus, could a combination of woody debris structures, GTR, and enhanced riparian management provide suitable habitat conditions for small mustelids, *M. gapperi*, and the overall forest-floor small mammal community in newly clearcut sites? We tested the hypotheses (H) that on newly clearcut sites, ($H_1$) the presence (index of activity patterns) of small mustelids, ($H_2$) abundance, species richness, and species diversity of the forest-floor small mammal community, and ($H_3$) reproduction of *M. gapperi* and *P. maniculatus*, would be greater on sites with the three retention treatments combined than on sites with no retention. A fourth hypothesis ($H_4$) predicted that the above response variables on sites with combined structural retention would be comparable to or higher than those in uncut old growth forest.

## 2. Methods

### 2.1. Study area

Our study was located in the Bald Range 25 km west of Summerland, BC ($49^0 40'$N; $119^0 53'$W) in the upper Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) ($IDF_{dk}$; d,k = dry precipitation and cool temperature regime) and Montane Spruce ($MS_{dm}$ ; d,m = dry precipitation and mild temperature regime) biogeoclimatic zones (Meidinger and Pojar, 1991). The area has sandy loam soils with gently rolling topography at 1450 to 1520 m elevation. The upper IDF and MS have a cool, continental climate with cold winters and moderately short, warm summers. The average temperature is below 0 °C for 2–5 months, and above 10 °C for 2–5 months, with mean annual precipitation ranging from 300 to 900 mm. Open to closed canopy mature forests of Douglas-fir cover much of the IDF zone, with even-aged post-fire lodgepole pine (*Pinus contorta* var. *latifolia*) stands at higher elevations. The MS landscape has extensive young and maturing seral stages of lodgepole pine, which have regenerated after wildfire 100–150 years ago. Hybrid interior spruce (*Picea glauca* × *P. engelmannii*) and subalpine fir (*Abies lasiocarpa*) are the dominant shade-tolerant climax trees. Trembling aspen (*Populus tremuloides*) is a common seral species and black cottonwood (*Populus trichocarpa*) occurs on some moist sites (Meidinger and Pojar, 1991).

The interior province-wide mountain pine beetle (MPB) (*Dendroctonus ponderosae*) epidemic passed through our study area in 2008 resulting in mortality ranging from 19% to 40% in lodgepole pine stands. Thus, salvage logging by clearcutting was conducted over 139 ha in the summer-fall of 2016. Prior to harvesting, stands were composed of a mixture of lodgepole pine with variable amounts of Douglas-fir, interior spruce, and subalpine fir. Mean ages of lodgepole pine ranged from 80 to 120 years and for Douglas-fir ranged from 120 to 220 years. Mean tree heights ranged from 10.5 to 19.5 m for lodgepole pine and from 16.7 to 27.5 m for Douglas-fir. Overall, approximately 30% of uncut old-growth forest remained in this area.

### 2.2. Experimental design

Four replicate blocks with a mean (±SE) area of 24.2 ± 1.3 ha (range 20.9 to 26.7 ha) were chosen from the areas clearcut in 2016. These blocks were separated by a mean (±SE) distance of 1.53 ± 0.46 km. A randomized complete block design had the following five treatments: (a) no structures with dispersed post-harvest debris only, (b) a linear array of woody debris piles, (c) a riparian unit, (d) Douglas-fir trees as aggregated retention (8–29 trees/ha), and (e) uncut old-growth forest (Figs. 1 and 2). The 20 sites (5 treatments × 4 replicates) were selected on the basis of operational scale, harvest sites that were the size of current forestry operations, and reasonable proximity of sites to one another. Mean area of sites on clearcut blocks ranged from 4.2 to 7.0 ha. Uncut forest sites were 5 to 20+ ha in area. All treatments within a block were reasonably separated to enhance statistical and biological independence (Hurlbert, 1984): a mean (±SE) of 0.34 ± 0.04 km (range

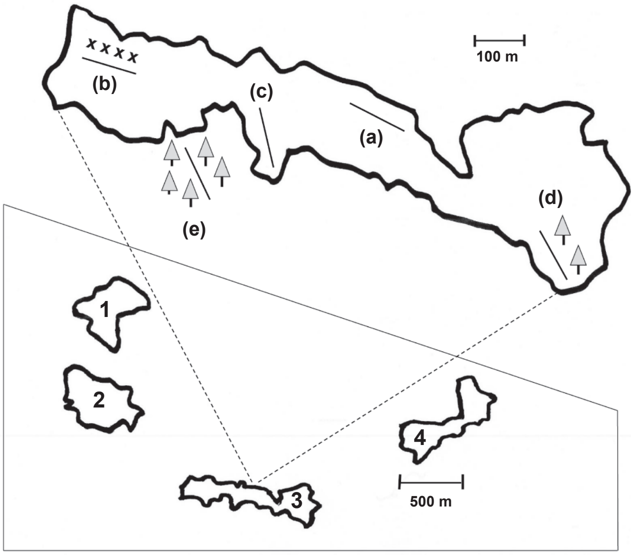

**Fig. 1.** Map of study area with four replicate blocks (1, 2, 3, and 4) and an example inset of the five treatments associated with one block: (a) dispersed woody debris, (b) piles of woody debris X X X X, (c) riparian, (d) green-tree retention, and (e) uncut forest. The transect for sampling mustelid presence and small mammal prey species is shown for each treatment site.

0.1–1.0 km). For the major small mammal species, a measure of this independence was that only 9 of 735 (1.2%) individual *M. gapperi* and 56 of 883 (6.3%) individual *P. maniculatus* were captured on more than one site. Treatment sites were not considered independent for marten, weasels, or *N. amoenus*.

### 2.3. Retention treatments

Timber harvesting was targeted at clearcut salvage of lodgepole pine after, or impending, MPB attack and any spruce and subalpine fir crop trees with some reserves of Douglas-fir trees as GTR units. All retention treatments were installed during harvesting in summer-autumn 2016. Volumes of downed wood (≥1 cm in diameter) in the dispersed treatments were measured using the line-intersect method of Van Wagner (1968) in three plots, each of which was an equilateral triangle with 20 m sides. Location of plots was randomly chosen along the small mammal sampling line on each site. Volumes of woody debris in piles were measured by the method of Hardy (1996), first estimating the volume of a pile and then using a biomass ratio (or bulk density factor) of 0.67 to estimate the net volume of woody biomass, after the method discussed in Sullivan et al. (2011). Mean (±SE) volume ($m^3$/ha) of debris was 163.7 ± 20.4 in the dispersed sites and 340.7 ± 83.8 in the piles sites. Piles of woody debris averaged 3.6 ± 0.1 m in height, 14.5 ± 0.2 m in diameter or width, and 141.8 ± 19.7 m in length. Mean (±SE) number of piles per site was 5.8 ± 0.6.

The riparian sites included small headwater streams < 1.5 m wide with deciduous trees (primarily trembling aspen) and advanced regeneration of coniferous trees, shrubs, and herbs maintained in a relatively undisturbed condition, but harvestable conifers were carefully removed (Fig. 1c). Riparian buffer reserves of overstory trees are not required on this common stream class that make up the majority of stream length in much of BC, and elsewhere in North America (Lowe and Likens, 2005; Bradley, 2020). Mean (±SE) width of the riparian zones was 15.6 ± 2.0 m and length was 217.5 ± 60.9 m. The GTR sites had a group of retention trees (ca. 1.0 ha in area) with some additional individual trees retained elsewhere on a given cutblock (Fig. 1d). Mean (±SE) density of Douglas-fir as retention trees per site was 3.5 ± 1.2/ha (range 1.2 to 6.9) with aggregated retention at a mean of 17.3 ± 5.0/ha (range of 8–29). Mean (±SE) density/ha of overstory coniferous trees in the uncut forest was 390 ± 91 per site and mean canopy closure was 89.9 ± 3.4%. There were no site preparation treatments on any of these harvested sites, prior to planting of a mixture of lodgepole pine, Douglas-fir, and interior spruce seedlings in 2017. Natural regeneration of subalpine fir and the other three coniferous species augmented the planting program.

### 2.4. Stand structure and understory vegetation

Sampling of coniferous tree species in layers in 0–1, 1–2, 2–3, and > 3 m height classes was done in a 5.64-m radius circular plot (100 $m^2$) located systematically at alternate trap stations along lines in the dispersed, riparian, GTR, and uncut forest sites (see below). A fifth class was added for overstory trees in the riparian, GTR, and uncut forest sites. In each plot, we counted trees in each height class by species, and measured dbh (diameter at breast height, 1.3 m above soil surface) and total height (digital hypsometer – Forestor Vertex) of selected overstory trees in the dominant and suppressed height classes. This sampling was not done in the debris piles sites since they were similar to the dispersed sites. Percentage canopy closure in the uncut forest was measured by four readings of a spherical densiometer (Englund et al., 2000) at each plot for a total of 20 measurements per stand.

Understory vascular plants were sampled on one 25-m transect consisting of five plots each containing two sizes of nested subplots: a 3-m × 3-m subplot for sampling shrubs and a 1-m × 1-m subplot for sampling herbs, systematically located in each site following the method of Lindgren and Sullivan (2013). Shrub and herb layers were subdivided into six height classes: 0–0.25, 0.25–0.5, 0.5–1.0, 1.0–2.0, 2.0–3.0, and 3.0–5.0 m. A visual estimate of percentage cover of the ground was made for each species height class combination within the appropriate nested subplot. These data were then used to calculate crown volume index ($m^3$/0.01 ha) for each plant species. The product of percent cover and representative height class value gives the volume of a cylindroid which represents the space occupied by the plant in the community. Crown volume index values were then averaged by species for each plot size and converted to 0.01-ha base for each species and layer.

Species richness was the total number of species sampled for the plant communities in each site (Krebs, 1999). Species diversity was represented by the Shannon-Wiener index. Structural diversity was based on the same indices as for species richness and diversity with the height classes of each of the herb and shrub layers acting as "species". This measure of habitat complexity utilized the same Shannon-Wiener index with plant species represented by height classes and the amount (crown volume index) of vegetation in each class. Density of trees in each height class was used in these calculations of structural diversity for coniferous trees (Sullivan et al., 2001). Plant species were identified in accordance with Parish et al. (1996). Sampling of understory vegetation and coniferous stand structure were done in July-August 2018 and 2019, respectively.

### 2.5. Presence of mustelids

The presence of mustelids was measured along the small mammal sampling line at each site by (a) observations, as well as live-trapping and release (marten and small weasels) (Fig. 1f), (b) fecal scats on three 30 × 30 cm plywood boards used as covers at trap stations, and (c) predation disturbance of small mammals at trap sites (Zielinski and Kucera, 1995; BC Ministry of Environment, 1998). Fecal scats were identified to marten or weasel according to Murie (1954) and Rezendes (1999). One Tomahawk live-trap (Model 201, Tomahawk Live trap Company, Tomahawk, Wisconsin) equipped with a nest box (1-L plastic bottle with coarse brown cotton) was located at each of three stations. Traps were baited with strawberry jam. Traps were set in the evening on day 1 and checked in the mornings of days 2 and 3. Sampling periods and intervals were identical to those described below for small mammal species. Counts of mustelid observations and live captures (marten and

**Fig. 2.** Photographs (summer 2018) of treatment sites in the structural retention study in south-central British Columbia, Canada: (a) dispersed woody debris, (b) piles of woody debris in a linear array, (c) riparian, (d) green-tree retention of Douglas-fir, (e) uncut old forest, and (f) short-tailed weasel.

weasels in Tomahawk traps and weasels in Longworth traps), fecal scats, and disturbance of live-traps were recorded during the 5–6 trapping periods each year. Predation disturbance of live-traps was readily identified to weasels or marten as other potential carnivores such as coyotes (*Canis latrans*) or lynx (*Lynx canadensis*) are uncommon in these habitats. Fecal scats may have been deposited at any time during the intervals between these trapping periods. All captured mustelids were identified to species and released.

### 2.6. Forest-floor small mammals

Forest-floor small mammals were sampled at 4-week intervals from May or June to October 2017, 2018, 2019, and 2020. Each of the 20 sites had a 143-m transect for efficient sampling of community composition of small mammals (Pearson and Ruggiero, 2003). Each transect had 10 trap stations at 14.3-m intervals with three Longworth live-traps at each station. Traps were supplied with whole oats, a slice of carrot, and cotton as bedding. Each trap had a 30-cm × 30-cm plywood cover for protection from sunlight (heat) and precipitation. Traps were set on the afternoon of day 1 and checked on the mornings of day 2 and day 3, and then locked open between trapping periods. All animals captured were ear-tagged with serially numbered tags, breeding condition noted, weighed on Pesola spring balances, and point of capture recorded. Breeding condition was noted by palpation of male testes and the condition of mammaries of the females (Krebs, 2013). Animals were released on the lines immediately after processing. Unfortunately, the overnight trapping technique resulted in a high mortality rate for shrews. Therefore, shrews were collected, frozen, and later identified according to tooth patterns (Nagorsen, 1996). All handling of animals followed guidelines approved by the American Society of Mammalogists (Sikes et al., 2016) and the Animal Care Committee, University of British Columbia.

### 2.7. Demographic and diversity parameters

Abundance estimates of the two major species (numerically dominant), the red-backed vole and deer mouse, were derived from the Jolly-Seber (J-S) stochastic model for open populations with small sample size corrections (Seber, 1982; Krebs, 1999). Minimum number alive was used to estimate populations of the long-tailed vole (*Microtus longicaudus*), meadow vole (*Microtus pennsylvanicus*), and heather vole (*Phenacomys intermedius*); number of individuals was used for the montane shrew (*S. monticolus*) and common shrew (S. *cinereus*). Number of individuals captured each trapping week was used for northwestern chipmunks (*N. amoenus*) owing to their occasional movements among lines. Overall, we consider these estimates to be an index of population size per line (Krebs et al., 2011). Jolly trappability was calculated for the major species according to the estimate discussed by Krebs and Boonstra (1984). Species richness was the total number of species sampled for the mammal communities in each site (Krebs, 1999). Species diversity was based on the Shannon-Wiener index which is well represented in the ecological literature (Burton et al., 1992). Mean annual measurements of abundance, species richness, and species diversity of small mammals were calculated using the estimated parameter for each species or community for a given sampling period and then averaged over the number of sampling periods for each year. There were four summer (May-October) and three winter (November-April) periods.

Mass (g) at sexual maturity was used to determine age classes of *M. gapperi*: juvenile = 1–18; adult $\geq$ 19; and *P. maniculatus*: juvenile = 1–20; adult $\geq$ 21 to assess reproduction and survival. Juveniles were considered to be young animals recruited during the study. Measurements of recruitment (new animals that entered the population through reproduction and immigration), number of successful pregnancies, and early juvenile productivity were derived from the sample of animals captured in each trapping session and then summed for each summer period. A pregnancy was considered successful if a female was lactating during the period following the estimated time of birth of a litter. Early juvenile productivity is an index relating recruitment of young into the trappable population to the number of lactating females (Krebs et al. 1969). A modified version of this index is number of juvenile animals at week $t$ divided by the number of lactating females caught in week $t - 4$.

### 2.8. Statistical analysis

A one-way analysis of variance (ANOVA) was used to detect differences among sites for abundance and diversity measurements for coniferous stand structure and understory vegetation (Zar, 1999). A repeated-measures analysis of variance (RM-ANOVA) (IBM Corp., 2019) was used initially to determine the effect of the five treatments on mean values for presence of mustelids, abundance of *M. gapperi*, *P. maniculatus*, *N. amoenus*, *M. longicaudus*, total shrews, total small mammals, species richness, and species diversity, as well as the effects of time and treatment × time interactions. The measurement of mustelid presence was a combined count of observations and captures, fecal scats, and predation disturbance of marten or small weasels for each replicate site and year. Meadow voles and heather voles had low and inconsistent sample sizes (<2/line), and hence precluded statistical analysis, but these species were included in total abundance summaries. This analysis was also conducted to detect differences in mean values for number of recruits and number of successful pregnancies for *M. gapperi* and *P. maniculatus*, as well as the effects of time and treatment × time interactions.

Another RM-ANOVA was then conducted to determine the effect of a combination of retention structures (piles of woody debris, riparian, and GTR) on mean values for combined counts of presence of mustelids and abundance of *M. gapperi*, *P. maniculatus*, *M. longicaudus*, total shrews, total small mammals, species richness, and species diversity compared with the dispersed (no retention) and uncut forest treatments. To standardize the response variables for the combined structures, we calculated the mean value of piles, riparian, and GTR variables for each replicate block, and then compared this value to those of the dispersed and uncut forest lines for that block. Homogeneity of variance was measured by the Levene statistic. Where significant treatment effects were detected that also had significant treatment × time interactions over the 4-year period, additional univariate ANOVAs were conducted within individual years. Mauchly's $W$-test statistic was used to test for sphericity (independence of data among repeated measures) (Littel, 1989; Kuehl, 1994). For data found to be correlated among years, the Huynh-Feldt (H-F) correction was used to adjust the degrees of freedom of the within-subjects $F$-ratio (Huynh and Feldt, 1976). Proportional data were transformed by arcsin square root (Fowler et al., 1998). Overall mean values ($n = 16$; 4 replicate sites × 4 years) ± 95% confidence intervals (CIs) were calculated for those response variables measured in the combined retention structures vs. the dispersed (no retention) and uncut forest treatments. Duncan's multiple range test (DMRT), adjusted for multiple contrasts, was used to compare mean values based on RM-ANOVA results (Saville, 1990). In all analyses, the level of significance was at least $P = 0.05$.

## 3. Results

### 3.1. Stand structure and understory vegetation

Mean (±SE) diameters (cm) and heights (m) of large overstory trees in the riparian, GTR, and uncut forest sites were 58.1 ± 5.4 and 28.8 ± 1.1 for Douglas-fir, 40.8 ± 6.4 and 23.9 ± 2.3 for spruce, 31.6 ± 3.6 and 21.9 ± 1.0 for subalpine fir, and 38.6 ± 1.0 and 26.5 ± 0.5 for trembling aspen. Windthrow of residual trees in riparian and GTR sites was < 10% over the 4-year study. Mean (±SE) diameters (cm) and heights (m) of suppressed overstory coniferous trees in the riparian sites were 14.1 ± 1.0 and 11.1 ± 1.5 for spruce and 12.8 ± 0.2 and 10.1 ± 1.0 for subalpine fir. Mean density of understory conifers was similar ($P = 0.55$) in the 0–1 m height class with comparable numbers of small trees among sites (Table 1). Although not formally significant ($P = 0.09$), mean density of conifers in the 1–2 m class was dominated by the riparian and uncut forest sites at 500 and 690 trees/ha, respectively. Similarly, there was a significant ($P \leq 0.04$) difference among sites for conifers in the 2–3 and > 3 m height classes with the riparian and uncut forest sites higher (DMRT; $P = 0.05$) than the dispersed and GTR sites which had few trees or none (Table 1). Mean total density and species diversity of understory conifers were similar ($P \geq 0.28$) among sites.

Mean abundance of herbaceous vegetation was significantly different among sites for both cover ($F_{4,12} = 11.83$; $P < 0.01$) and crown volume index ($F_{4,12} = 7.70$; $P < 0.01$) with the riparian sites having 4.2 to 12.9 times higher (DMRT; $P = 0.05$) amounts than the other sites (Table 1; Fig. 3a). Mean abundance of shrubs was similar ($P \geq 0.11$) among sites for both cover and volume. However, the riparian sites had 1.1 to 5.2 (cover) and 2.9 to 33.3 (volume) times more shrubs than the other sites which may have biological significance despite the inherent variability among sites (Fig. 3b). Mean total species richness of herbs and shrubs was significantly ($F_{4,12} = 3.34$; $P = 0.05$) different among sites with the riparian higher (DMRT; $P = 0.05$) than the dispersed and uncut forest sites, but similar to the piles and GTR sites (Table 1). Mean total species diversity of herbs and shrubs approached significance ($F_{4,12} = 3.15$; $P = 0.055$) ranging from 1.77 (uncut forest) to 3.14 (piles).

Mean total structural diversity of herbs and shrubs was significantly ($F_{4,12} = 3.83$; $P = 0.03$) different among sites with the riparian similar to the dispersed and uncut forest but 3.3 to 4.1 times higher (DMRT; $P = 0.05$) than the piles and GTR (Table 1; Fig. 4a). Similarly, mean structural diversity of conifers was significantly ($F_{3,9} = 8.53$; $P < 0.01$) different among sites with the uncut forest and riparian sites similar and the forest higher (DMRT; $P = 0.05$) than the dispersed and GTR sites (Table 1; Fig. 4b).

**Table 1**
Mean ($n = 4$ replicate sites) ± SE abundance and diversity measurements of understory coniferous trees and vegetation in the five treatment sites at the Summerland study area and results of univariate ANOVA analyses. Mean values followed by different letters are significantly different by DMRT. Significant values are given in bold text.

| | Treatment | | | | | Analysis | |
|---|---|---|---|---|---|---|---|
| Parameter | Dispersed woody debris | Piles of woody debris | Riparian | Green-tree retention | Uncut forest | | |
| Understory conifers (trees/ha) | | | | | | $F_{3,9}$ | $P$ |
| 0–1 m height class | 3435 ± 1251 | – | 2570 ± 591 | 1435 ± 842 | 2320 ± 869 | 0.75 | 0.55 |
| 1–2 m height class | 50 ± 21 | – | 500 ± 286 | 15 ± 15 | 690 ± 230 | 3.04 | 0.09 |
| 2–3 m height class | 5 ± 5b | – | 235 ± 139ab | 0 ± 0b | 335 ± 57a | 4.33 | **0.04** |
| > 3 m height class | 0 ± 0b | – | 240 ± 134ab | 0 ± 0b | 1175 ± 317a | 10.56 | **< 0.01** |
| Total conifers | 3490 ± 1265 | – | 3545 ± 888 | 1450 ± 839 | 4520 ± 822 | 1.51 | 0.28 |
| Species diversity | 1.15 ± 0.07 | – | 0.95 ± 0.16 | 0.94 ± 0.08 | 0.81 ± 0.25 | 0.64 | 0.61 |
| Structural diversity | 0.12 ± 0.05b | – | 0.85 ± 0.39ab | 0.09 ± 0.09b | 1.53 ± 0.16a | 8.53 | **< 0.01** |
| Understory vegetation | | | | | | $F_{4,12}$ | $P$ |
| Herbs – cover ($m^2$/0.01 ha) | 10.2 ± 1.9b | 13.5 ± 6.8b | 56.4 ± 10.1a | 8.3 ± 1.6b | 5.4 ± 2.5b | 11.83 | **< 0.01** |
| Herbs – volume ($m^3$/0.01 ha) | 3.5 ± 0.9b | 4.1 ± 2.1b | 22.0 ± 6.3a | 2.4 ± 0.5b | 1.7 ± 0.9b | 7.70 | **< 0.01** |
| Shrubs – cover ($m^2$/0.01 ha) | 19.5 ± 8.0 | 6.4 ± 1.6 | 21.9 ± 10.4 | 4.2 ± 1.1 | 13.5 ± 4.9 | 2.39 | 0.11 |
| Shrubs – volume ($m^3$/0.01 ha) | 9.3 ± 6.0 | 1.7 ± 0.5 | 36.6 ± 25.6 | 1.1 ± 0.3 | 12.7 ± 7.4 | 1.85 | 0.19 |
| Total species richness | 11.3 ± 1.2b | 16.5 ± 3.8ab | 20.0 ± 2.0a | 13.0 ± 1.5ab | 9.0 ± 1.9b | 3.34 | **0.05** |
| Total species diversity | 2.37 ± 0.32 | 3.14 ± 0.23 | 2.42 ± 0.29 | 2.74 ± 0.26 | 1.77 ± 0.30 | 3.15 | 0.06 |
| Total structural diversity | 0.95 ± 0.28abc | 0.44 ± 0.15bc | 1.45 ± 0.30a | 0.35 ± 0.15c | 1.22 ± 0.49ab | 3.83 | **0.03** |

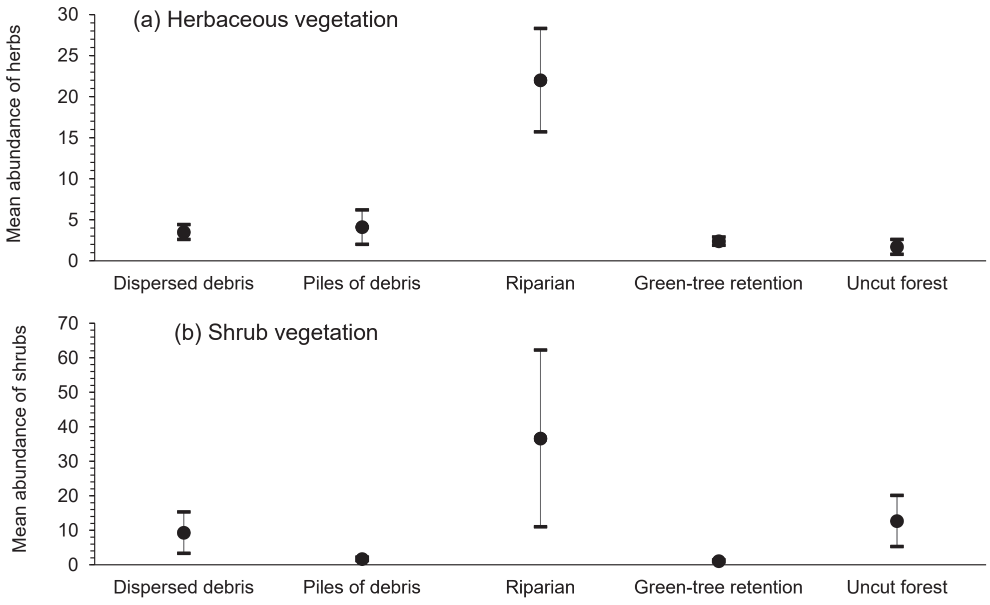

**Fig. 3.** Mean ($n = 4$ replicate sites) ± SE abundance of (a) herbaceous and (b) shrub vegetation in the dispersed, piles, riparian, green-tree retention, and uncut forest sites during 2017–2020 in the study of structural retention on new clearcuts.

### 3.2. *Presence of mustelids*

Mean presence of mustelids was statistically similar ($F_{4,12} = 2.51$; $P = 0.10$) among sites. However, in terms of overall mustelid activity, the piles and riparian sites had 2.0 to 4.0 and 1.8 to 3.7 times as many counts, respectively, as the other three sites and may have biological significance (Table 2; Fig. 5). The composite parts of this measurement were: mustelid captures or observations (1 marten and 50 weasels), fecal scats (0 marten and 17 weasels), and disturbed traps (5 marten and 15 weasels). Mean counts of mustelid presence per sampling period ranged from 0.15 to 0.55 in the sites with woody debris piles and from 0.20 to 0.50 in the riparian sites (Table 2). Mean counts of mustelid presence ranged from 0.04 to 0.10, 0 to 0.20, and 0.10 to 0.33 for the dispersed, GTR, and forest sites, respectively. Overall counts for all sites per year were reasonably consistent: 2017–20; 2018–26; 2019–17; and 2020–25. There were no significant ($P \geq 0.84$) time or treatment × time interaction effects.

### 3.3. *Abundance of small mammal prey species*

A total of eight species of forest-floor small mammals, composed of 2881 individuals, were captured in 21 trapping periods. *P. maniculatus* was the most common species captured with 883 individuals, followed by *M. gapperi* (735), *N. amoenus* (466), *S. monticolus* (386), *M. longicaudus* (302), *M. pennsylvanicus* (42), *S. cinereus* (37), and *P. intermedius* (30). Susceptibility to capture was measured by Jolly trappability estimates with mean (±SE) values ranging from 73.3 ± 4.7% to 77.9 ± 9.0% for *M. gapperi*; 67.1 ± 5.5% to 84.6 ± 1.0% for *P. maniculatus*; and was 81.0 ± 3.2% for *M. longicaudus* in those sites where these species were common.

Mean abundance of *M. gapperi* was significantly ($F_{4,12} = 11.10$; $P < 0.01$) different among treatment sites with the piles and uncut forest sites at consistently higher (DMRT; $P = 0.05$) numbers (2.3 to 22.8 times on average) than the other sites (Table 3; Fig. 6). In 2017, populations of red-backed voles reached a mean annual peak of 22 per line in the piles and then declined in subsequent years to peaks of 3 to 13 voles per line

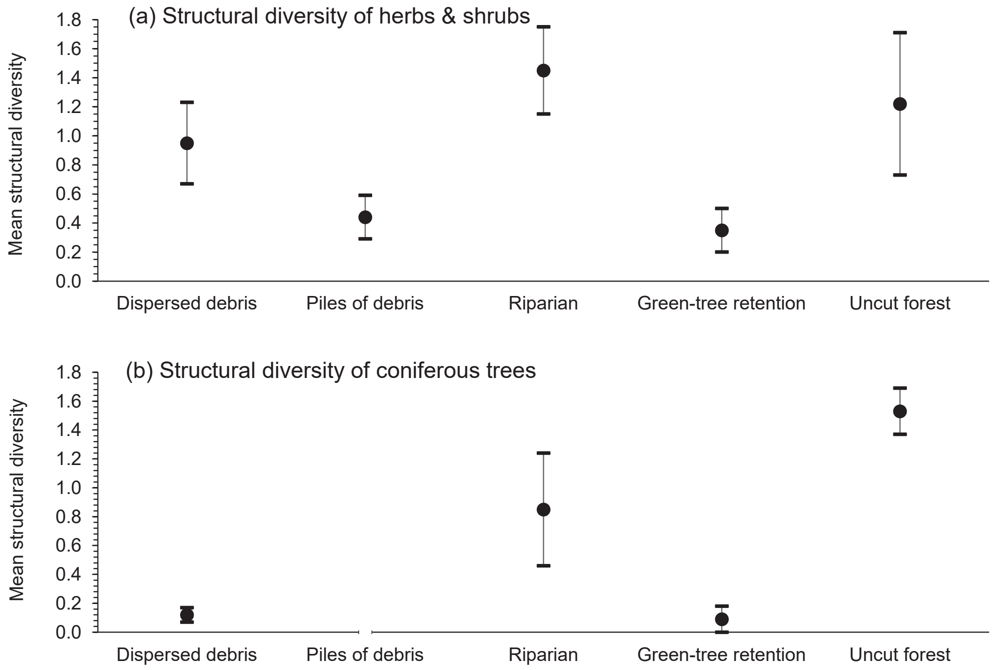

**Fig. 4.** Mean ($n$ = 4 replicate sites) ± SE structural diversity of (a) total herbs and shrubs and (b) coniferous trees in the dispersed, piles, riparian, green-tree retention, and uncut forest sites during 2017–2020 in the study of structural retention on new clearcuts.

**Table 2**
Annual mean ($n = 4$ replicate sites) ± SE presence of mustelids (based on live captures, fecal scats, and trap disturbance per sampling period and year) per line in the five treatment sites at the Summerland study area, and results of RM-ANOVA. $F$-values identified by * were calculated using an H-F correction factor, which decreased the stated degrees of freedom due to correlation among repeated measures.

| | Treatment | | | | | Treatment | | Time | | Treatment × time | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Dispersed woody debris | Piles of woody debris | Riparian | GTR[1] | Uncut forest | $F_{4,12}$ | $P$ | $F_{3,45}$ | $P$ | $F_{12,45}$ | $P$ |
| 2017 | 0.10 ± 0.06 | 0.55 ± 0.36 | 0.25 ± 0.13 | 0.00 ± 0.00 | 0.10 ± 0.10 | 2.51 | 0.10 | 0.17* | 0.84 | 0.38* | 0.95 |
| 2018 | 0.10 ± 0.10 | 0.45 ± 0.26 | 0.20 ± 0.12 | 0.20 ± 0.12 | 0.35 ± 0.10 | | | | | | |
| 2019 | 0.10 ± 0.10 | 0.15 ± 0.05 | 0.35 ± 0.24 | 0.10 ± 0.06 | 0.15 ± 0.10 | | | | | | |
| 2020 | 0.04 ± 0.04 | 0.29 ± 0.12 | 0.50 ± 0.28 | 0.08 ± 0.05 | 0.13 ± 0.08 | | | | | | |
| Overall ($n = 16$) | 0.09 ± 0.04 | 0.36 ± 0.11 | 0.33 ± 0.10 | 0.10 ± 0.04 | 0.18 ± 0.05 | | | | | | |

[1] GTR = Green-tree retention.

and this change with time was significant ($F_{3,45} = 31.07$; $P < 0.01$) and consistent across sites (Fig. 6). Mean numbers of *M. gapperi* in dispersed and riparian sites were consistently less than 5 animals per line over the study. A significant treatment × time interaction effect was related to the change to comparable levels of abundance in the piles and uncut forest from 2018 to 2020 and the dramatic decline in numbers of *M. gapperi* in the GTR sites in late 2018 and thereafter (Table 3; Fig. 6).

Mean abundance of *P. maniculatus* was significantly ($F_{4,12} = 6.15$; $P < 0.01$) different among treatment sites with almost consistently higher (DMRT; $P = 0.05$) numbers (1.5 to 2.5 times) in the dispersed and GTR sites than the other sites (Table 3; Fig. 7). *P. maniculatus* reached mean annual peak numbers of 11–17 per line in 2019. A significant ($F_{3,45} = 41.97$; $P < 0.01$) time effect was particularly dramatic in 2019 when deer mouse numbers increased on all sites before declining to less than one-half the mean numbers in 2020.

Mean abundance of *N. amoenus* was significantly ($F_{4,12} = 10.21$; $P < 0.01$) different among treatment sites with consistently higher (DMRT; $P = 0.05$) numbers (1.3 to 3.5 times) in the GTR than the other sites (Table 3). Mean annual peak numbers of *N. amoenus* were at 6 to 9 chipmunks per line during 2018–2020. Mean numbers of northwestern chipmunks increased significantly ($F_{3,45} = 18.04$; $P < 0.01$) with time in all sites (Table 3).

Although at relatively low mean abundance (<1 vole/line) in the dispersed and uncut forest sites, mean numbers of *M. longicaudus* were significantly ($F_{4,12} = 3.57$; $P = 0.04$) different among sites with the piles dominating and the riparian sites secondarily, in 2017–2018, having higher (DMRT; $P = 0.05$) numbers of voles (Table 3). Mean abundance of total shrews was similar ($P = 0.09$) among sites, consistently < 5 animals per trapping period and line (Table 3). The riparian sites tended to have more (1.6 to 4.3 times) shrews, on average, than the other sites and this may have biological significance.

### 3.4. Total abundance, species richness, and diversity

Mean abundance of total small mammals was significantly ($F_{4,12} = 8.06$; $P < 0.01$) different among sites with consistently higher (DMRT; $P = 0.05$) numbers (1.4 to 2.0 times) in the piles than other sites (Table 3; Fig. 8). Mean annual peak numbers of total mammals in the piles sites reached 32 and 26 per line in 2017 and 2019, respectively (Fig. 8). These numbers were matched by mean annual peaks of 26 and 17 total mammals in the GTR sites in 2019 and 2020, respectively. Significant ($P < 0.01$) time and treatment × time interaction effects were related to the general decline in mean abundance of total mammals in the piles and uncut forest sites and the decline and increase in mammals in the dispersed and GTR sites. Mean abundance in the riparian sites was remarkably consistent ranging from 9 to 12 mammals per line over the four years (Table 3). Mean species richness ($F_{4,12} = 9.81$; $P < 0.01$) and species diversity ($F_{4,12} = 6.64$; $P < 0.01$) were significantly different

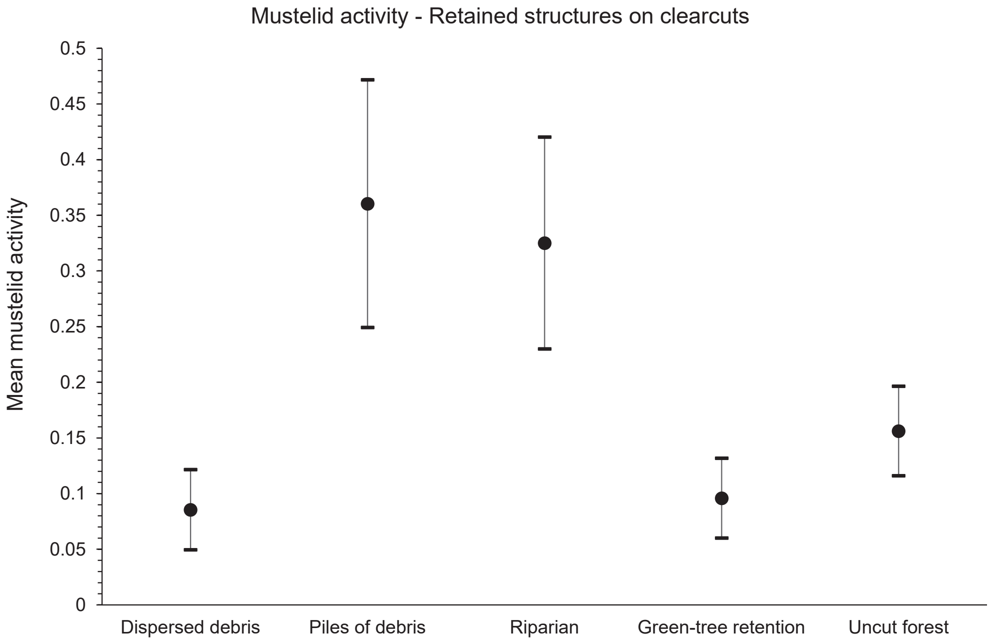

**Fig. 5.** Mean ($n = 4$ replicate sites) ± SE mustelid activity in the dispersed, piles, riparian, green-tree retention, and uncut forest sites during 2017–2020 in the study of structural retention on new clearcuts.

among sites with consistently higher (DMRT; $P = 0.05$) levels (1.1 to 1.7 times) in the piles and riparian sites than other sites (Table 3).

### 3.5. Combined structural retention and mammals

Mean presence of mustelids was statistically similar ($F_{2,6} = 3.84$; $P = 0.08$) among the combined structural treatments (piles + riparian + GTR) and the dispersed and uncut forest sites (Table 4). However, it may be biologically important that the overall mean mustelid presence in the combined treatments was 2.9 and 1.4 times higher than that in the dispersed and uncut forest sites, respectively. There were no time or treatment × time interaction effects for this analysis of mustelid presence.

Mean abundance of *M. gapperi* was significantly ($F_{2,6} = 28.54$; $P < 0.01$) different among sites with higher (DMRT; $P = 0.05$) overall mean numbers (11.1 to 16.6 times) in the combined retention and uncut forest sites than the dispersed sites (Table 4). In addition, the uncut forest had significantly (DMRT; $P = 0.05$) more (1.6 times) *M. gapperi* than the combined retention. A significant treatment × time interaction was reflected in the variable pattern among treatments for decline in numbers of red-backed voles over the four years (Fig. 6). The univariate analysis indicated a consistent significant ($P \leq 0.04$) difference among the three treatments each year with the combined retention and uncut forest sites similar in mean abundance of *M. gapperi* in 3 of 4 years.

Mean abundance of *P. maniculatus* was significantly ($F_{2,6} = 10.60$; $P = 0.01$) different among sites with higher (DMRT; $P = 0.05$) overall mean numbers in the dispersed than uncut forest, and numbers of deer mice similar in the combined retention to both of the other treatments (Table 4). Mean abundance of *N. amoenus* was significantly ($F_{2,6} = 8.05$; $P = 0.02$) different among sites with higher (DMRT; $P = 0.05$) overall mean numbers (2.3 to 2.6 times) in the dispersed and combined retention sites than the uncut forest. A significant treatment × time interaction was evident in the univariate analyses where all sites were similar in mean number of northwestern chipmunks in 2017–2018 but diverged in 2019–2020 to the same pattern as the overall analysis. Mean abundances of *M. longicaudus* ($F_{2,6} = 11.94$; $P < 0.01$) and total shrews ($F_{2,6} = 9.50$; $P = 0.01$) were significantly different among sites with higher (DMRT; $P = 0.05$) overall mean numbers in the sites with combined retention than either of the dispersed or uncut forest sites (Table 4).

Similarly, mean total abundance, species richness, and species diversity were all significantly ($P \leq 0.03$) different among sites with the combined retention sites at a range of 1.3 to 1.6 times higher (DMRT; $P = 0.05$) than the dispersed and uncut forest sites (Table 4). Univariate analyses for the significant treatment × time interaction indicated that total small mammals in the combined retention and uncut forest sites were higher (DMRT; $P = 0.05$) in mean total abundance than in the dispersed sites in 2017–2018. This pattern then changed to the dispersed and combined retention sites being higher in abundance than the forest in 2019, and almost in 2020 ($P = 0.07$).

The significant time effects in this combined retention analysis followed the same patterns for species and parameters as those described for the initial analysis of the five treatments (Tables 3 and 4).

### 3.6. Reproduction and survival of M. gapperi and P. maniculatus

Mean recruitment of *M. gapperi* was significantly ($P \leq 0.02$) different among sites with higher (DMRT; $P = 0.05$) overall numbers of juvenile (8.4 to 10.4 times) and adult (8.2 to 12.4 times) voles in the combined retention and uncut forest sites than the dispersed sites (Table 5). Sample size of *M. gapperi* in the dispersed sites was insufficient to be included in this analysis. These recruit numbers declined significantly ($P \leq 0.01$) with time as observed in the population decline of *M. gapperi* over the study (Fig. 6). The significant treatment × time interactions indicated that for both age classes of voles, the difference among sites was maintained for the first three years before similar numbers of recruits were recorded in the combined retention and uncut forest sites in 2020. Mean number of successful pregnancies was also significantly ($F_{2,6} = 13.90$; $P < 0.01$) different among sites with the combined retention and uncut forest sites higher (9.9 to 11.4 times) (DMRT; $P = 0.05$) than the dispersed sites (Table 5). The mean index of juvenile productivity of *M. gapperi* was similar ($P = 0.20$) among the three sites.

Mean numbers of recruits of *P. maniculatus* were similar among sites for juvenile mice but significantly ($F_{2,6} = 11.77$; $P < 0.01$) different for total recruits with the dispersed and combined retention sites higher (1.6 to 1.9 times) (DMRT; $P = 0.05$) than the uncut forest sites (Table 5). Mean number of successful pregnancies and index of juvenile productivity were also significantly ($P \leq 0.02$) different among sites with the dispersed and combined retention sites higher (12.4 to 18.7 times)

**Table 3**
Mean ($n = 4$ replicate sites) ± SE annual abundance for each species, total abundance, and species richness, and diversity per ha within the forest-floor small mammal community for the 2017–2020 period among the five treatment sites at the Summerland study area, and results of RM-ANOVA. *F*-values identified by * were calculated using an H-F correction factor, which decreased the stated degrees of freedom due to correlation among repeated measures. Within a row, columns of mean values with different letters (upper-case for RM-ANOVA; lower-case for univariate ANOVA) are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts. Significant values are given in bold text.

| | | | | | | RM-ANOVA | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Treatment | | | | | Treatment | | Time | | Treatment × time | |
| Parameter and year | Dispersed | Piles | Riparian | GTR[1] | Uncut forest | $F_{4,12}$ | *P* | $F_{3,45}$ | *P* | $F_{12,45}$ | *P* |
| Mean abundance | | | | | | | | | | | |
| *M. gapperi* | **B** | **A** | **B** | **B** | **A** | 11.19 | **<0.01** | 31.07* | **<0.01** | 4.11* | **<0.01** |
| 2017 | 1.1d ± 0.7 | 17.5a ± 3.2 | 3.1 cd ± 1.1 | 7.6bc ± 0.5 | 9.8b ± 1.3 | | | | | | |
| 2018 | 0.5b ± 0.3 | 10.8a ± 2.0 | 1.7b ± 1.1 | 3.3b ± 0.8 | 10.0a ± 1.9 | | | | | | |
| 2019 | 0.0b ± 0.0 | 4.7a ± 1.6 | 0.4b ± 0.3 | 0.5b ± 0.5 | 3.0a ± 0.8 | | | | | | |
| 2020 | 0.0b ± 0.0 | 2.3a ± 1.4 | 0.2b ± 0.2 | 0.1b ± 0.1 | 3.0a ± 1.2 | | | | | | |
| *P. maniculatus* | **A** | **AB** | **B** | **A** | **B** | 6.15 | **<0.01** | 41.97 | **<0.01** | 1.18 | 0.33 |
| 2017 | 5.2 ± 1.8 | 2.3 ± 0.3 | 1.5 ± 0.4 | 3.2 ± 1.2 | 1.4 ± 0.8 | | | | | | |
| 2018 | 2.5 ± 0.3 | 0.2 ± 0.1 | 0.7 ± 0.4 | 1.8 ± 0.5 | 0.2 ± 0.1 | | | | | | |
| 2019 | 10.5 ± 0.8 | 8.4 ± 1.1 | 5.2 ± 1.6 | 10.5 ± 1.5 | 4.5 ± 1.4 | | | | | | |
| 2020 | 5.0 ± 0.7 | 4.8 ± 1.0 | 2.7 ± 1.0 | 6.8 ± 1.3 | 3.3 ± 0.6 | | | | | | |
| *N. amoenus* | **B** | **BC** | **AB** | **A** | **C** | 10.21 | **<0.01** | 18.04 | **<0.01** | 1.56 | 0.14 |
| 2017 | 1.7 ± 0.8 | 1.2 ± 0.5 | 2.0 ± 0.3 | 2.0 ± 0.3 | 1.2 ± 0.3 | | | | | | |
| 2018 | 1.8 ± 0.4 | 0.8 ± 0.3 | 2.6 ± 0.8 | 3.0 ± 0.8 | 1.2 ± 0.3 | | | | | | |
| 2019 | 3.6 ± 0.5 | 2.8 ± 0.6 | 4.0 ± 0.4 | 5.4 ± 0.6 | 0.7 ± 0.2 | | | | | | |
| 2020 | 4.0 ± 0.8 | 3.4 ± 0.8 | 4.2 ± 0.6 | 6.5 ± 0.4 | 1.9 ± 0.4 | | | | | | |
| *M. longicaudus* | **B** | **A** | **AB** | **B** | **B** | 3.57 | **0.04** | 2.79* | 0.07 | 0.73* | 0.69 |
| 2017 | 0.1 ± 0.1 | 3.6 ± 1.3 | 1.9 ± 1.1 | 0.8 ± 0.5 | 0.0 ± 0.0 | | | | | | |
| 2018 | 0.4 ± 0.2 | 4.7 ± 2.1 | 3.2 ± 2.0 | 1.5 ± 0.7 | 0.1 ± 0.1 | | | | | | |
| 2019 | 0.2 ± 0.2 | 4.2 ± 1.6 | 0.4 ± 0.4 | 0.7 ± 0.6 | 0.0 ± 0.0 | | | | | | |
| 2020 | 0.1 ± 0.1 | 2.6 ± 0.9 | 0.1 ± 0.1 | 0.3 ± 0.3 | 0.0 ± 0.0 | | | | | | |
| Total shrews | | | | | | 2.56 | 0.09 | 5.91 | **<0.01** | 1.38 | 0.21 |
| 2017 | 1.3 ± 0.2 | 1.2 ± 0.1 | 3.1 ± 0.7 | 1.2 ± 0.9 | 1.0 ± 0.3 | | | | | | |
| 2018 | 0.2 ± 0.1 | 0.6 ± 0.1 | 1.4 ± 0.4 | 0.4 ± 0.2 | 0.4 ± 0.1 | | | | | | |
| 2019 | 0.6 ± 0.1 | 1.0 ± 0.3 | 1.7 ± 0.6 | 1.1 ± 0.7 | 0.1 ± 0.1 | | | | | | |
| 2020 | 0.3 ± 0.1 | 1.8 ± 0.5 | 1.2 ± 0.3 | 1.5 ± 1.1 | 0.3 ± 0.2 | | | | | | |
| Total small mammals | **B** | **A** | **B** | **B** | **B** | 8.06 | **<0.01** | 9.66 | **<0.01** | 3.26 | **<0.01** |
| 2017 | | | | | | | | | | | |
| 2018 | 9.8b ± 1.2 | 25.7a ± 1.8 | 11.8b ± 1.7 | 14.8b ± 2.1 | 13.4b ± 2.1 | | | | | | |
| 2019 | 5.9c ± 1.0 | 17.1a ± 1.4 | 10.3bc ± 2.2 | 10.1bc ± 1.2 | 11.7b ± 2.1 | | | | | | |
| 2020 | 14.8b ± 1.0 | 21.1a ± 1.2 | 12.0bc ± 2.3 | 17.7ab ± 2.7 | 8.3c ± 1.6 | | | | | | |
| | 9.5b ± 1.3 | 15.0a ± 2.2 | 9.1b ± 1.0 | 15.3a ± 2.7 | 8.4b ± 1.1 | | | | | | |
| Species richness | **CD** | **A** | **AB** | **BC** | **D** | 9.81 | **<0.01** | 3.08 | **0.04** | 1.39 | 0.21 |
| 2017 | | | | | | | | | | | |
| 2018 | 3.05 ± 0.22 | 4.15 ± 0.13 | 4.00 ± 0.24 | 3.60 ± 0.55 | 2.75 ± 0.29 | | | | | | |
| 2019 | 2.65 ± 0.35 | 3.10 ± 0.17 | 3.55 ± 0.67 | 3.25 ± 0.29 | 2.15 ± 0.22 | | | | | | |
| 2020 | 2.40 ± 0.16 | 4.45 ± 0.21 | 3.40 ± 0.42 | 2.95 ± 0.38 | 2.20 ± 0.14 | | | | | | |
| | 2.29 ± 0.04 | 4.42 ± 0.24 | 2.96 ± 0.51 | 2.84 ± 0.45 | 2.63 ± 0.19 | | | | | | |
| Species diversity | **BC** | **A** | **A** | **AB** | **C** | 6.64 | **<0.01** | 2.29 | 0.09 | 2.89 | **<0.01** |
| 2017 | | | | | | | | | | | |
| 2018 | 1.30 ± 0.17 | 1.31 ± 0.17 | 1.68 ± 0.13 | 1.44 ± 0.21 | 0.95 ± 0.10 | | | | | | |
| 2019 | 1.17a ± 0.19 | 1.02ab ± 0.16 | 1.38a ± 0.23 | 1.39a ± 0.13 | 0.60b ± 0.06 | | | | | | |
| 2020 | 0.88c ± 0.12 | 1.80a ± 0.05 | 1.40b ± 0.12 | 1.15bc ± 0.15 | 0.79c ± 0.12 | | | | | | |
| | 1.03b ± 0.03 | 1.85a ± 0.06 | 1.23b ± 0.29 | 1.23b ± 0.15 | 1.12b ± 0.08 | | | | | | |

[1] GTR = Green-tree retention.

(DMRT; $P = 0.05$) than the uncut forest sites.

## 4. Discussion

### 4.1. Stand structure and understory vegetation

Among the five treatment sites, the riparian and uncut forest had similar profiles of understory conifers in terms of density and structural diversity. Overstory conifers were maintained in the uncut forest and somewhat in the GTR sites, whereas the riparian sites had a few large trees but were primarily composed of advanced coniferous regeneration. The availability of moisture throughout the growing season and removal of overstory cover of coniferous trees resulted in substantial growth and diversity of herbs and shrubs in the riparian sites which reflected one of the many unique features of these ecosystems (Gregory et al., 1991; Naiman et al., 1993; Kauffman et al., 2001). Studies of vegetation recovery after clearcut harvesting of headwater streams in northern Ontario and western Washington found no immediate effect on species richness or diversity but advocated the importance of careful removal of trees with limited disturbance (Wilk et al., 2010; Newaz et al., 2019). In addition, the similarly high total species richness of herbs and shrubs in the piles, riparian, and GTR sites likely contributed to the efficacy of these sites in terms of the combined structural retention providing mammal habitats.

### 4.2. Presence of mustelids

Although not formally significant ($P = 0.08$), our results for mustelid presence tended to support $H_1$ that these small carnivores would occur more frequently on sites with combined structural treatments (piles + riparian + GTR) than the dispersed and uncut forest sites. Assessment of all sites clearly indicated that the debris piles and riparian units dominated the pattern of presence of small mustelids. In addition, the combined retention sites had substantial populations of small mammal prey.

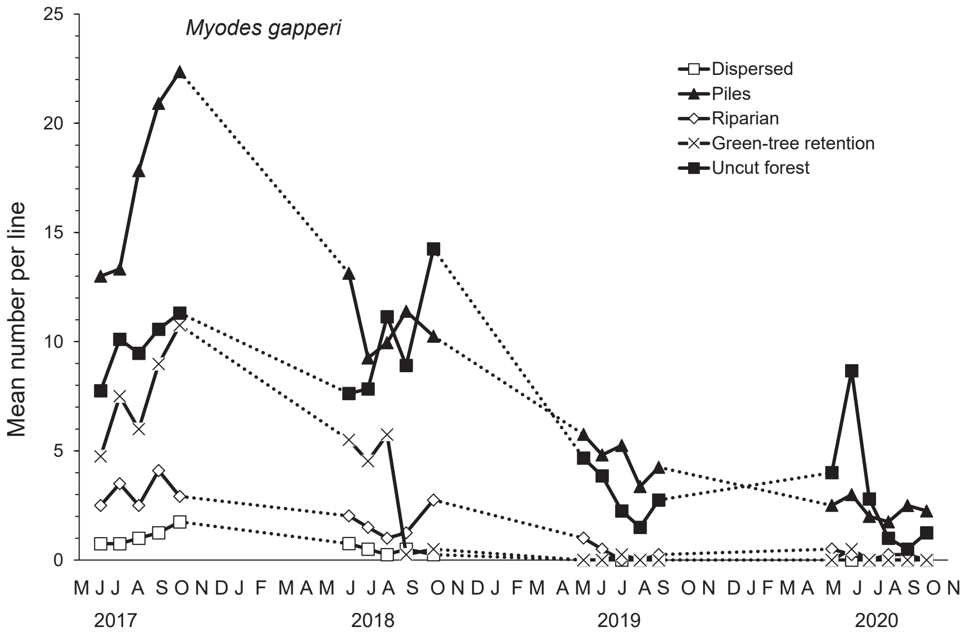

**Fig. 6.** Mean ($n = 4$ replicate sites) number of *Myodes gapperi* per line as an index based on Jolly-Seber population estimates in the dispersed, piles, riparian, green-tree retention, and uncut forest sites during 2017–2020. Data points indicate individual trapping weeks each summer (May to October) and dots indicate winter periods when populations were not sampled.

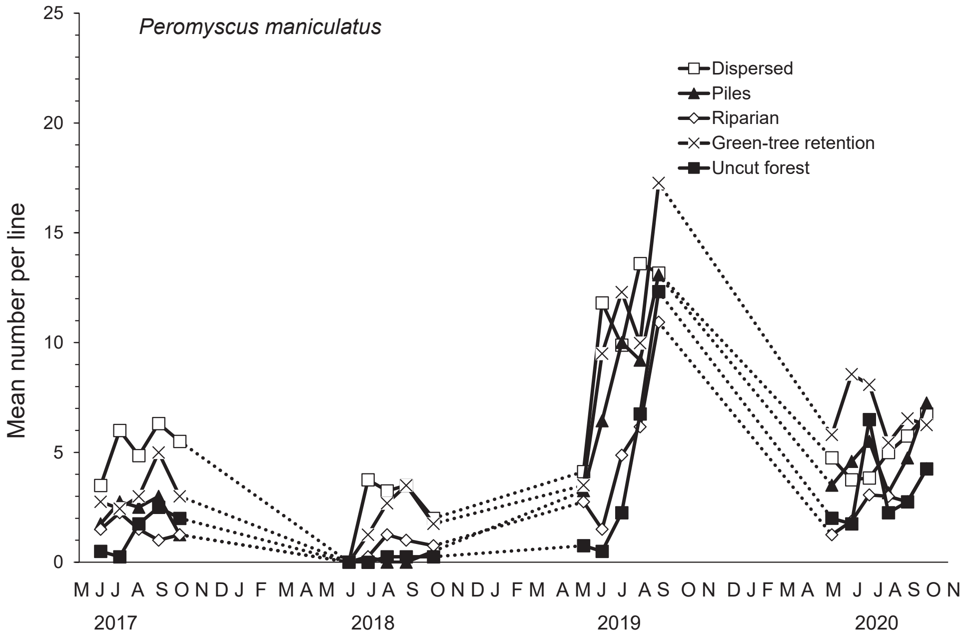

**Fig. 7.** Mean ($n = 4$ replicate sites) number of *Peromyscus maniculatus* per line as an index based on Jolly-Seber population estimates in the dispersed, piles, riparian, green-tree retention, and uncut forest sites during 2017–2020. Data points indicate individual trapping weeks each summer (May to October) and dots indicate winter periods when populations were not sampled.

The linear nature of riparian sites and rows of piles provided both cover and small mammal prey, and hence likely provided secure pathways for dispersal movements of mustelids (Buskirk and Zielinski, 2003; Linnell et al., 2017; Mougeot et al., 2020). Similar results were reported for marten, short-tailed weasels, and their small mammal prey in upland and riparian strips on new clearcuts in Quebec (Darveau et al., 2001; Potvin and Bertrand, 2004). The GTR sites were similar to the dispersed sites in terms of lack of security cover at ground level, and hence few mustelids occurred there. Constructed piles or aggregations of coarse woody debris seem to be required as focal points for small mustelids to find mammal prey species such as red-backed voles (Lisgo et al., 2002; Andruskiw et al., 2008; Bunnell and Houde, 2010). Indeed, our woody debris piles showed substantial use by mustelids as also reported for these structures elsewhere (Sullivan et al., 2017a; Seip et al., 2018).

### 4.3. Abundance and diversity of small mammal prey species

The overall high total numbers of small mammal prey species supported $H_2$ that abundance would be greater on sites with the three retention treatments combined than on the dispersed sites with no

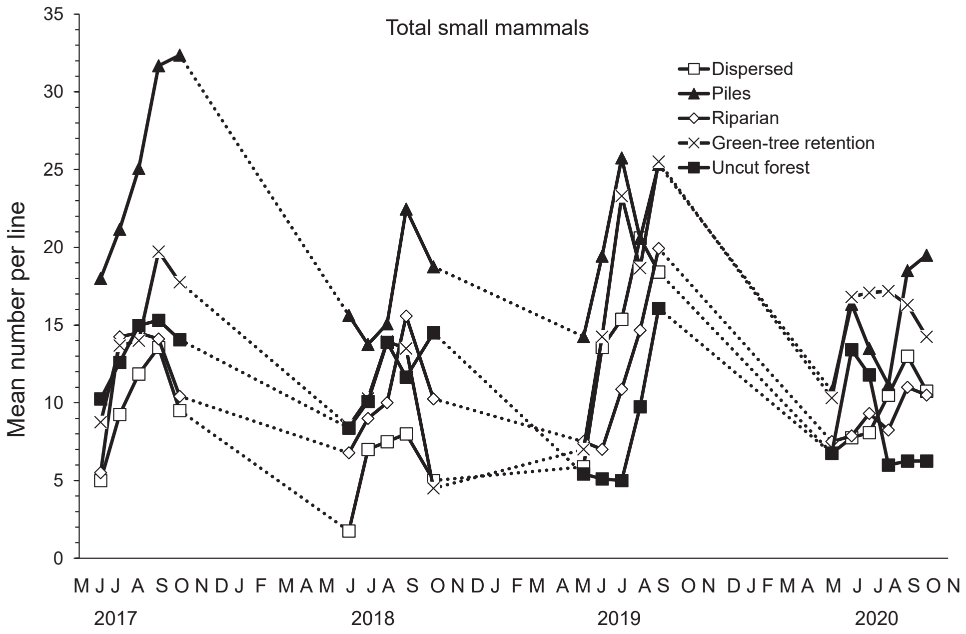

**Fig. 8.** Mean ($n = 4$ replicate sites) number of total small mammals per line as an index based on total population estimates in the dispersed, piles, riparian, green-tree retention, and uncut forest sites during 2017–2020. Data points indicate individual trapping weeks each summer (May to October) and dots indicate winter periods when populations were not sampled.

**Table 4**
Overall mean ($n = 16$; 4 replicate sites × 4 years) ± SE presence of mustelids and abundance for each species, total abundance, species richness, and diversity per line within the forest-floor small mammal community for the 2017–2020 period among three treatment sites (dispersed, combined piles + riparian + GTR, and uncut forest) at the Summerland study area, and results of RM-ANOVA. *F*-values identified by * were calculated using an H-F correction factor, which decreased the stated degrees of freedom due to correlation among repeated measures. Within a row, columns of mean values with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts. Significant values are given in bold text. [1] GTR = Green-tree retention.

| | | | | RM-ANOVA | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Treatment | | | Treatment | | Time | | Treatment × time | |
| Parameter | Dispersed | Combined Piles + Riparian + GTR[1] | Uncut forest | $F_{2,6}$ | *P* | $F_{3,27}$ | *P* | $F_{6,27}$ | *P* |
| Overall mean presence | | | | | | | | | |
| Mustelids | 0.09 ± 0.04 | 0.26 ± 0.05 | 0.18 ± 0.05 | 3.84 | 0.08 | 0.46 | 0.71 | 0.35 | 0.90 |
| Overall abundance | | | | | | | | | |
| *M. gapperi* | 0.39c ± 0.20 | 4.31b ± 0.91 | 6.46a ± 1.07 | 28.54 | **<0.01** | 14.73 | **<0.01** | 3.03 | **0.02** |
| *P. maniculatus* | 5.81a ± 0.89 | 4.01ab ± 0.77 | 2.33b ± 0.58 | 10.60 | **0.01** | 22.02 | **<0.01** | 1.08 | 0.40 |
| *N. amoenus* | 2.77a ± 0.40 | 3.13a ± 0.37 | 1.22b ± 0.17 | 8.05 | **0.02** | 14.78 | **<0.01** | 3.16 | **0.02** |
| *M. longicaudus* | 0.17b ± 0.07 | 2.00a ± 0.33 | 0.01b ± 0.01 | 11.94 | **<0.01** | 3.61* | **0.04** | 2.35* | 0.07 |
| Total shrews | 0.59b ± 0.12 | 1.33a ± 0.19 | 0.43b ± 0.12 | 9.50 | **0.01** | 10.16 | **<0.01** | 1.15 | 0.36 |
| Total small mammals | 9.98b ± 0.96 | 15.00a ± 0.77 | 10.46b ± 0.98 | 6.68 | **0.03** | 5.03* | **<0.01** | 3.66* | **0.01** |
| Species richness | 2.60b ± 0.13 | 3.55a ± 0.14 | 2.43b ± 0.12 | 19.77 | **<0.01** | 3.57 | **0.03** | 0.79 | 0.59 |
| Species diversity | 1.09b ± 0.08 | 1.40a ± 0.05 | 0.86b ± 0.07 | 13.09 | **<0.01** | 3.01 | **0.05** | 2.01 | 0.10 |

retention. When all sites were analyzed together, total abundance in the piles and GTR was consistently higher or the same as the dispersed and uncut forest sites. The riparian sites were similar to either of the dispersed or uncut forest, and hence the combined retention sites provided the most suitable habitat conditions overall. The composition of total mammals was dominated (72.3%) by three species: *M. gapperi*, *P. maniculatus*, and *N. amoenus*. The consistently high populations of *M. gapperi* in combined retention and uncut forest sites also supported $H_2$. In particular, the initial dramatic response of *M. gapperi* to the debris piles was similar to other reports of constructed piles and windrows of post-harvest debris on new clearcuts (Lisgo et al., 2002; Fauteux et al., 2012; Seip et al., 2018; Sullivan and Sullivan, 2019). The initial comparable numbers of red-backed voles on GTR sites to uncut forest in 2017–2018 before declining to low numbers was also reported by Sullivan and Sullivan (2001) for similar levels of aggregated retention of Douglas-fir trees in a nearby study area. Partially cut forests with GTR levels of >15 $m^2$/ha BA or 30% uncut forest across a variety of forest ecosystems have maintained suitable habitat for *M. gapperi* in some cases (Steventon et al., 1998; Von Treba et al., 1998; Moses and Boutin, 2001; Fuller et al., 2004; Gitzen et al., 2007, and others).

A similar pattern of higher relative numbers of *M. gapperi* in 2017–2018 than later years occurred in the riparian sites as well. The dramatic population changes in *M. gapperi* over the four years was likely related to the 6- to 7-year population fluctuation of this microtine (Sullivan et al., 2017b). Peak populations of mean abundance of 14 to 21 voles per ha were recorded in our long-term independent uncut forest sites in 2017–2018 (Sullivan and Sullivan, 2019), before declining to low (<5 per ha) numbers in 2019–2020. Another contributing factor could be the residual red-backed voles that survived clearcutting of the original forest and dispersed to available habitats that included our treatment sites.

The generalist species *P. maniculatus* and *N. amoenus* were maintained in the combined retention sites at levels similar to the dispersed sites and generally higher than the uncut forest, and hence did not

**Table 5**
Overall mean ($n = 16$; 4 replicate sites × 4 years) ± SE demographic attributes for *M. gapperi* and *P. maniculatus* for the 2017–2020 period among three treatment sites (dispersed, combined piles + riparian + GTR, and uncut forest) at the Summerland study area, and results of RM-ANOVA. *F*-values identified by * were calculated using an H-F correction factor, which decreased the stated degrees of freedom due to correlation among repeated measures. Within a row, columns of mean values with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts. Significant values are given in bold text. GTR[1] = Green-tree retention.

| | Treatment | | | RM-ANOVA | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Treatment | | Time | | Treatment × time | |
| Species + parameter | Dispersed | Piles + Riparian + GTR[1] | Uncut forest | | | | | | |
| *M. gapperi* | | | | $F_{2,6}$ | *P* | $F_{3,27}$ | *P* | $F_{6,27}$ | *P* |
| Juvenile recruits | 0.63b ± 0.40 | 5.31a ± 1.36 | 6.56a ± 1.71 | 9.11 | **0.02** | 8.05* | **0.01** | 3.25* | **0.05** |
| Total recruits | 1.25c ± 0.70 | 10.27b ± 2.42 | 15.50a ± 2.80 | 25.95 | **<0.01** | 15.92* | **<0.01** | 3.86* | **0.03** |
| Pregnancies | 0.31b ± 0.18 | 3.56a ± 0.69 | 3.06a ± 0.73 | 13.90 | **<0.01** | 4.69* | **0.02** | 1.35* | 0.28 |
| Juvenile productivity | 0.50 ± 0.38 | 1.09 ± 0.25 | 1.97 ± 0.86 | 2.10 | 0.20 | 1.30* | 0.30 | 0.55* | 0.70 |
| *P. maniculatus* | | | | $F_{2,6}$ | *P* | $F_{3,27}$ | *P* | $F_{6,27}$ | *P* |
| Juvenile recruits | 8.94 ± 1.47 | 7.50 ± 1.55 | 6.25 ± 1.56 | 3.84 | 0.08 | 23.65 | **<0.01** | 0.08 | 1.00 |
| Total recruits | 14.06a ± 1.80 | 11.54a ± 2.02 | 7.31b ± 1.63 | 11.77 | **<0.01** | 19.32 | **<0.01** | 0.22 | 0.97 |
| Pregnancies | 3.56a ± 0.63 | 2.92a ± 0.64 | 0.19b ± 0.19 | 7.31 | **0.02** | 3.38 | **0.03** | 0.98 | 0.46 |
| Juvenile productivity | 2.11a ± 0.40 | 3.09a ± 0.57 | 0.17b ± 0.17 | 14.38 | **<0.01** | 1.63* | 0.21 | 1.32* | 0.29 |

support the prediction of $H_2$. *P. maniculatus* tends to be widespread among the various early-successional habitats associated with post-clearcut landscapes (Gitzen et al., 2007; Wilk et al., 2010). The dramatic increase in numbers of deer mice in 2019 may have been related to declining numbers of *M. gapperi* possibly owing to interspecific competition (Lemaitre et al., 2010). *N. amoenus* again showed a pattern of preference for the GTR sites (Sullivan et al., 2008) and these results were reported elsewhere for *Neotamias* spp. and structural complexity of vegetation, downed wood, and tree retention (Waldien et al., 2006; Gray et al., 2019; Sultaire et al., 2021). *M. longicaudus* and total shrews did fit the prediction of $H_2$ with the three retention sites providing suitable habitat. Similar results were reported for *M. longicaudus* in long-term (up to 12 years) measurements of debris structures (Sullivan and Sullivan, 2019) and riparian areas (Smolen and Keller, 1987). *S. monticolus* was at higher abundance in debris structures than dispersed sites (Sullivan et al., 2017a) in south-central BC and was strongly associated with riparian zones in Oregon and Washington (Doyle, 1990). The measurements of species richness and diversity in the combined retention sites reflected the same pattern as for the individual treatments and further supported the prediction of $H_2$.

### 4.4. Reproduction and survival of *M. gapperi* and *P. maniculatus*

Several authors have noted that counts of small mammals as abundance or density per unit area may not be a sound measure of habitat quality, particularly where changes in forest succession or management occur (Van Horne, 1983; Wheatley et al., 2002; Martineau et al., 2016; Nelson et al., 2019). Demographic parameters such as reproduction and survival also need to be investigated rather than just short-term measures of relative abundance and habitat associations (Anthony et al., 2003). Our $H_3$ that reproductive attributes for *M. gapperi* and *P. maniculatus* would be greater on sites with combined structural retention than on sites with no retention seemed to be supported in part for *M. gapperi*. The generalist *P. maniculatus* had greater reproduction in the combined retention and dispersed (no retention) sites than the uncut forest, and hence also provided partial support, albeit the converse of the prediction of $H_3$. These measurements of reproduction essentially paralleled the abundance metrics for both species. Thus, the combined retention sites did provide quality habitats on new clearcuts, at least for these two major species in the first four years after harvest.

### 4.5. Structural retention and uncut forest

The prediction of $H_4$ that response variables on sites with combined retention would be comparable to or higher than those in uncut forest was supported for mean total abundance in 2017–2018. However, this pattern changed in 2019 (and nearly so in 2020) whereby mean total abundance in the combined retention and dispersed sites were higher than the uncut forest. The influx of generalist species that occupy early successional sites after clearcutting and decline of the specialist closed-canopy *M. gapperi* were the driving factors in this change (Fisher and Wilkinson, 2005; Zwolak, 2009).

### 4.6. Study limitations

We chose clearcut blocks that had the five treatments in reasonably close but still independent proximity to one another. Douglas-fir was the dominant residual tree in GTR sites in mixed lodgepole pine – Douglas-fir forest in this ecological zone. The dispersed or aggregated patterns and locations were dependent on the number and distribution of Douglas-fir in the original forest before harvest. Thus, not every clearcut unit necessarily had any retention stands of Douglas-fir. Similarly, only certain clearcut units had riparian zones associated with small headwater streams or other moisture-receiving areas. The third retention treatment of post-harvest debris piles was dependent on a linear array of piles that were conserved and not located near main haul roads or other access points of human activity and the risk of fire, albeit minor. Thus, selection of replicate blocks with these treatments was quite targeted and inferences from our results should be cautiously extrapolated to other forestry operations and ecological zones.

Ideally, we would have liked to have had equivalent numbers of replicate (e.g., $n = 3$) dispersed and uncut forest sites within each block to correspond with the combined retention treatment which was a mean value of the piles + riparian + GTR units. However, this would have increased the overall number of sites from 20 to 36 which was beyond the logistical and funding possibilities of the study. Another addition that may have strengthened the study was a riparian treatment with a forested buffer zone. However, such treatments were relatively uncommon with the small headwater streams in these IDF and MS ecological zones. Thus, we chose to study riparian units that had reasonably careful removal of harvestable conifers with minimal disturbance of advanced coniferous regeneration and understory vegetation. Responses of small mammals to a forested riparian buffer may have been similar to the uncut forest sites although buffer width would be crucial as reported by Marczak et al. (2010) and Wilk et al. (2010).

As noted, our treatment sites were all assumed to be independent replicates within a given block, at least with respect to the small mammal species, other than *N. amoenus* and the mustelids. Thus, we did not pursue population estimation for *N. amoenus* but relied on number of chipmunks captured in a given trapping period. As noted, very few *M. gapperi* and *P. maniculatus* were captured on more than one site. In addition, measurements of mean maximum distance moved were estimated from sampling of grid systems in nearby study areas (Sullivan and Sullivan, 2019): *M. gapperi* 22.0 m, *P. maniculatus* 39.2 m and *M. longicaudus* 20.0 m. At least for these species, the mean (±SE) distance between sites of 0.34 ± 0.04 km would seem to provide a strong foundation for our assumption of independence.

Similarly, for our measurements of mustelid presence, we tallied number of incidences of captures or observations, fecal scats, and predation events rather than estimating abundance for each of the three species. In terms of ecological scale, mean home ranges of *M. erminea* were reported to be 65–205 ha in post-harvest mixed-wood forest sites in Alberta (Lisgo, 1999). Thus, our measurements were essentially an index of activity patterns with more signs of mustelid presence likely being representative of higher activity in that part of a given block. In addition, it is important to note that these inferences reflect mustelid and small mammal prey responses to habitat structures during summer and fall (May to October) only, and in the first fours years post-clearcutting. Responses to these treatments may not have been the same during other seasons of the year and in subsequent years.

## 5. Conclusions

Clearcutting continues to dominate as a harvesting system in temperate and boreal forests. We asked what multiple enhancements of stand structure could be done at the time of clearcutting to provide food and cover for mustelids and prey species. This quest is crucial as partial harvesting efforts via GTR leave relatively low numbers of retention trees (e.g. $< 5$ $m^2$/ha basal area or 5% uncut forest), owing primarily to economic constraints. Our study is the first to measure the responses of small mustelids and small mammal prey species to combined structural retention using woody debris piles of post-harvest residues, enhanced riparian management, and green-tree retention on a given cutblock. These structural retention sites were generally more attractive to mustelids than either of the dispersed debris (no retention) or uncut forest. Mean overall mustelid presence was 1.8–4.0 times higher in the piles and riparian sites than that in the other three sites. Mean numbers of individual mammal prey species were highest in debris piles and uncut forest (*M. gapperi*), dispersed and GTR sites (*P. maniculatus* and *N. amoenus*), piles and riparian sites (*M. longicaudus*), and riparian sites (*Sorex* spp.). Mean total abundance, species richness, and species diversity of small mammal prey species were 1.3 to 1.6 times higher in the combined retention than the dispersed and uncut forest sites.

Thus, all of these structural retention treatments accommodate at least one or more species of small mammal prey and where available should increase abundance and diversity on new clearcuts. Debris piles and riparian sites clearly provide mustelids with cover, dispersal paths, and focal points for finding prey. In addition, it may be possible that one or more of our retention treatments may be combined on-site with one another (e.g., debris piles with GTR or near riparian zones). One or more of these retention treatments is highly recommended during most harvesting regimes in these forests.

## CRediT authorship contribution statement

**Thomas P. Sullivan:** Conceptualization, Methodology, Writing - original draft, Visualization, Investigation. **Druscilla S. Sullivan:** Data curation, Writing - review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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